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BOTANICAL GAZETTE

SEPTEMBER, 1902

THE RISE OF THE TRANSPIRATION STREAM: AN
HISTORICAL AND CRITICAL DISCUSSION.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY.
XXXVIII.

EDWIN BINGHAM COPELAND.

(WITH ONE FIGURE)

1. "Le phénomène de l'ascension de la sève est resté jusqu'à nos jours sans aucune explication plausible," wrote Dutrochet in 1837. Knight had said the same thing in 1801. During the intervening century there have been a considerable number of explanations, plausible enough to satisfy their authors, and a very few which have commanded a wide but temporary adherence. Every theory proposed has been overthrown by direct experiment, or shown to be in conflict with generally accepted principles of physics.

The work of Dixon and Joly and of Askenasy during the past decade has extended the knowledge already possessed in physics as to the cohesive power of water, and by the application of this knowledge these authors have developed a theory which has since almost monopolized the field. Believing that the true solution was to be found in this direction, I set up an apparatus intended to illustrate its application more strikingly than had been done before. This artificial tree had so much in its behavior in common with real trees that when all was done I was likewise unable to explain it.

Thirty-one pieces of glass tubing, each 3^{mm} in diameter and

about 40^{cm} long, were filled with plaster of Paris. As the plaster began to set they were put in a dish of boiled water. They were then boiled, cooled, and boiled again, boiled hard altogether two hours, and left in the same water over night. Air could be located by reflection between the plaster and the glass, as isolated bubbles, making on an average probably one-fifth to one-fourth of the area; the amount of air remaining in this way varied in different tubes. These tubes were connected with heavy rubber tubing; this was done by filling the rubber connections with fresh plaster paste and immediately forcing this out with the pieces of glass tubing to be connected. A continuous tube of plaster of Paris was thus made 12.4^m in height, reaching up the well surrounded by three flights of stairs in the Hull Botanical Laboratory. Four meters below the top was a T tube full of plaster, whose free arm was closed. The lower end was connected with a U tube full of water and mercury in equilibrium; this represented the root. At the top, above another T tube full of plaster with the free arm closed, was the leaf—a sort of inverted osmometer made by filling a funnel with plaster containing some K_4FeCN_6 , tying over it four sheets of parchment paper soaked in K_4FeCN_6 , sealing a glass wall around this, and filling the cup thus formed with a concentrated solution of $CuSO_4$ and $NaCl$. The surface of liquid exposed was great enough so that in the dry, warm air in the hall evaporation was more rapid than the loss was supplied, so that after the first day there was a slow precipitation, and after several days more water had to be added to forestall drying.

The experiment was started at 3:18 P. M., January 14. I recorded with very numerous measurements the rise of mercury in the closed arm of the U tube, most of which measurements it would be a waste of space to publish. The rise was without break or considerable irregularity. It was:

Until January 14, 4:18 P. M.,	3.0 ^{mm}	Until January 17, 3:18 P. M.,	128.0 ^{mm}
Until January 15, 3:18 P. M.,	64.5	Until January 18, 3:18 P. M.,	150.5
Until January 16, 3:18 P. M.,	101.5		

To obtain the decrease in tension in this manometer these

figures must of course be doubled, the suction developed during five days being then 301^{mm}.

From the very beginning of the absorption of water from the U tube this was a successful demonstration that a column of water above 10^m high in a porous substance, even in the presence of free air, will not break under its own weight. In addition to this it was very soon evident from the lifting of the mercury that maintaining its continuity did not strain it to near the breaking point. With the removal of water from the tube and the elevation of the mercury at its lower end, the tension of the air in the tube of course diminished and the bubbles expanded. During these five days, however, the expansion was not sufficient to cause any general confluence of the bubbles, even in the upper end of the tube.

At 3:18 P. M., January 18, the leaf was removed and the upper end of the tube closed tightly. The height of the mercury thereafter was:

January 18, 4:18 P. M., 151.5 ^{mm}	January 19, 11:30 A. M., 155.5 ^{mm}
January 18, 9:10 P. M., 155.0	January 19, 3:18 P. M., 157.0

The cause of this rise must be sought in the elasticity of the air in the tube. By virtue of this elasticity the suction of the leaf is—to employ materialization as a figure of speech—stored up, and only gradually transmitted to the root. Expressed in terms used with natural trees, transpiration and absorption are not necessarily parallel. This stored up suction is probably represented purely by the rise of 5^{mm} before January 19, 11:30 A. M. The subsequent more rapid rise I ascribe to the fact that the temperature of the hall fell very decidedly that afternoon. Such an effect of cooling, and the opposite result of warming, appeared at some other times.

That the tube could take up more water if the pressure—one atmosphere *minus* 314^{mm} of mercury—at the bottom were increased was evident; still, I thought it worth demonstrating. To this end mercury was poured into the free arm of the U tube until it stood even in both arms. At the same time the T tube 4^m from the top was opened and connected with a capillary

tube 1^m long full of water, whose lower end was in a mercury bath. This was done at 3.40 P. M., January 19. The height of the mercury was :

At the bottom	4 ^m from the top
January 19, 7:20 P. M., 9.0 ^{mm}	450 ^{mm}
January 20, 9:50 P. M., 28.5	530

The suction at the bottom was then 57^{mm}. At 1 P. M. the connection at 4^m had sprung a leak. It was unfair to compare tubes of such different caliber, so the U tube was replaced by a capillary of the same bore as the other, as nearly as possible, and arranged like it. Starting at 1:15 P. M., January 20, the height of the mercury was :

At the bottom	4 ^m from the top
January 20, 3:45 P. M., 130 ^{mm}	455 ^{mm}
6:25 P. M., 186	494
9:10 P. M., 252	531
January 21, 10:30 A. M., 326	550

On January 23 at 10:30 A. M., bubbles having twice been removed from the connection, the mercury at the bottom reached 428^{mm}.

The experiments continued about two months, during which I took several pages of measurements. At one time I arranged the osmometer so as to record the volume of water it absorbed, and found again that for a limited time it could be withdrawn from the tube very much faster than it was taken up lower down. I tried to determine the difference in the suction at the three openings in the tube when the mercury should be drawn up at each until they were in equilibrium; but this was reached so slowly that if there was no other accident, air always came out of the main tube and interfered. During the whole time that the experiment lasted there was a gradual increase in the air in the tube, and with this a decrease in the difference in tension at different heights.

The experiment ended with closing the T tube connections and setting the root end in a solution of eosin. As the eosin rose slowly in the tube, it was very easy to see that it left air between the plaster and the glass; rather more air than was

there when the apparatus was set up, but still so little that it was in small isolated flat bubbles.

While no experiment with any kind of an artificial tube can have the force of a demonstration as to what occurs in a real tree, the behavior of this apparatus was like that in trees as we know it, not only in the general achievement of the elevation of water to a still undefined height, but also in enough known details to make it most probable that the same fundamental physical principles are operative in both cases. But as already said, an analysis showing the elementary factors by which the water is raised has baffled me, even in my own apparatus.

The motive idea in setting up the apparatus—that the cohesion of the water in the tube must be responsible for any suction exerted more than 10^m below the top—was certainly a mistake. This is shown by the readings of the manometers higher up, and also by the continued rise of the mercury at the bottom, after suction at the top ceased, January 18. Both of these observations indicate that the suction developed in the tube is not as great as one atmosphere; that a difference in pressure of less than one atmosphere between top and bottom will lift water much more than 10^m under the peculiar conditions here present. But how? It might be that when water is drawn from the top of the tube it rarefies the air there, and that the suction so arising is propagated downward as largely as possible by the air, and that the bubbles and as little water as possible separating them are thus put in motion. In this way the suction necessary to lift the water should be only equal to that of a column of water equal to the total height of the indices separating the bubbles. But I did not observe that the bubbles moved, and my doubt as to their doing so is very much strengthened by the final observation that the rise of the eosin solution did not drive all the air before it. The tube did become more full of air in the upper part; but I think this was chiefly due to greater suction there, this causing the air present to occupy more space, and hastening diffusion inward through the rubber connections; and two of the “leaves” used leaked. It may be taken

as a fact that in wood there is no general upward movement of free air. Therefore, if it is believed that the behavior of this tube depends on the movement of the bubbles, the experiment is not appropriate to the problem. I shall show that the cohesion explanation is open to exactly the same objections in nature which disqualify it in this tube. This leaves a true explanation to be sought outside of the cohesion of the water, or the rise of the bubbles; by analogy this is probably true in my experiment.

The missing link in the problem is some play of surface tension. Assuming for the moment that the suction is transmitted largely by the air and that the bubbles are carried upward, there is still present continuous water in the plaster, and the upper end of this column would then be subject to the pull of its own 12^m of water, *plus* the suction at the bottom. Its surface tension—which I would rather call capillarity than cohesion here—might enable it to endure this strain. As a matter of fact, though, the tension of the water in the plaster and that of the air and the water around it at the same height must be practically the same. And since the surface tension opposes the movement of the bubbles, but not that of the water, it is natural that the latter should move when either must.

Any further discussion here would be duplicated in sifting the theories on the ascent of sap in nature. The positive result of our experiment is that the water column being continuous, but air being present, a suction of less than one atmosphere can still operate as a suction more than 12^m lower down.

There is an immense mass of published experimentation on the rise of the transpiration stream, whose results are not doubted. During the last four years I have repeated a large part of it for the sake of first-hand familiarity. I shall not add to the literature by republishing work already unquestioned.

II. Dutrochet, in the work quoted in the introduction, says that two forces cooperate to raise the sap: one of repulsion, osmotic in its nature, in the roots; and one of attraction, which is also osmosis—Dutrochet calls it endosmosis—in the leaves.

The driving force in the ascent of sap is root pressure. Seve-

ral explanations of its mechanism are conceivable. A suggestion by Pfeffer, that an unequal distribution within the cell of its osmotically active matter could cause a stream through the cell, has sometimes been adopted as the best solution. But to maintain this inequality would use as much, or rather more, energy than is required to keep up the osmotic pressure present and to lift the water however far it is forced; and this energy would presumably be a net loss to the plant. Detmer (1877) and C. Kraus regarded root pressure as a function of tissue tensions; but the tensions to be observed do not justify this view; and if they did, the solution would not be ultimate, for how should the tissue tensions arise and be maintained? Under the most advantageous conditions external to the active cells, a rhythmic variation in their permeability would result in a root pressure corresponding to the loss of osmotically active matter. But this would make an exceedingly poor machine, unless, as in the original scheme of this kind, by Godlewski, an unequal distribution of the permeability works with the periodic variation. And unequal permeability of different sides of the cell constitutes a perfectly sufficient explanation without any periodicity.

The greatest pressure must be exerted on the side of the cell where resistance to the passage of the solute is greatest. By virtue of this greater pressure when the cell can contain no more water, water will be taken up there, and given off on the other, more permeable side, with at least as much of the solute as would exert an osmotic pressure equal to that under which the water escapes. Artificial cells illustrating this mechanism have been constructed by Sachs (1882) and myself (1900).¹ In so far as its diffusion out of the tracheae into the cortex is resisted, the matter dissolved in the sap in the tracheae exerts an osmotic pressure against the surrounding cells, and to that extent a root pressure can then be maintained without any subsequent loss of solutes by the living cells. It seems probable to me that this suggestion represents the mechanism of the bleeding

¹ Hofmeister's artificial cell (1858: 11; 1862: 145), sometimes referred to as illustrating this action, had all its membranes alike.

of trees in spring better than does the preceding one. The two are closely related, and it would be difficult to distinguish them by experiment. Both have the source of energy in the concentration of the sap. Either provides for only a limited period of high pressure, while the supply of stored, dissolved, or soluble material in the root is carried away by the sap. In its essential features this explanation of the mechanism of root pressure was offered by Brücke in 1844. He illustrated (pp. 194-6) the proportionality of the concentration of the sap to the pressure observed, and said: "Wir werden in der Folge in einer andern Abhandlung näher betrachten, wie sich die Zellen vermittelst dieser löslichen und aufquellenden Substanzen zuerst strotzend mit Wasser anfüllen, und wie dann, in dem sie immer noch mehr Wasser anziehen, das was sie in ihrer Höhle nicht mehr beherbergen können, mit einem Theile der gelösten Substanzen als Saft in die benachbarten Spiralröhren hineingepresst wird." I cannot find that the treatise promised here ever appeared.

The parallel between pressure and concentration is illustrated again by the well-known use of the sap of birch and maple, trees with high root pressure, as sources of sugar. Clark (1874:188) found a root pressure in a *Betula lenta* seventy feet high sufficient to lift water 84.77 feet, the pressure in a root being higher yet. *Acer saccharinum*, with 3.57 per cent. sugar in its sap, registered a pressure of 31.73 feet of water. Clark also reports a pressure of 49.52 feet—6.5 feet above Hale's figure—by grape, the sap being sweet to the taste. The curve given by Schröder (1865) for the concentration of the sap of birch during the season and Clark's for the pressure are parallel, though the inorganic solute decreases constantly. The same author (Schröder, 1869:280) finds 3.44 per cent. sugar in the sap of *Acer platanoides*. The bleeding sap of walnut contains 4 per cent. sugar (Hartig, 1862:88). In all bleeding trees the concentration of the sap and the pressure are supposed to decrease together. In the herbs also (Ulbricht) the concentration of the sap decreases as bleeding goes on. Almost all publications on the concentration of the sap are in such terms that it is impossible to compute the

osmotic strength with any approach to exactness, but they still indicate that it is far more than sufficient to account for the accompanying pressure. On the other side is a statement by Duchartre (1859) that the water guttated by *Colocasia* is almost like distilled. The analysis was by Berthelot, who found traces of KCl, CaCO_3 , and organic matter. The earlier statement by Schmidt, who does not seem to have evaporated the water, that the guttated fluid is chemically pure water, is discordant with all modern results. Unger (1858) found 0.056 per cent. of solid matter in it. For other literature see Burgerstein (1889:405). To account osmotically for this guttation the water would have to be more concentrated than that absorbed by the roots by perhaps 0.03 per cent. of KCl.

According to Strasburger (1891:851), "Belegzellen" are rich in content during the time of bleeding, but not afterward. Still, Strasburger doubts their passing this content into the tracheae, and so setting up a root pressure; but his reason against this seems to be chiefly *a priori*, and based on the unsound assumption that the cells would be obliged to lose the sap in the same concentration in which they hold it.

In herbs, especially in young seedlings, it is very common to find bleeding or guttation during only a part of each day. The same plants in which guttated drops are found in the morning are likely to contain air under a decidedly diminished pressure in the afternoon. The reason is that the roots cannot furnish water as rapidly as it evaporates. But it is also possible that the activity of the roots is less by day, the removal of the hydrostatic pressure in the tracheae stimulating the active cells to become less permeable to their solutes on that side, and so economize their contents when it would be useless to let it escape. Labillardière, according to various text-books, says the palm *Arenga saccharifera* bleeds a sap richer in sugar by night than by day. The daily periodicity in pressure occurs also in trees. The bleeding of *Carpinus* (Strasburger, 1891:841) begins during the night and ceases before noon. Birches may also cease to bleed before noon (Detmer, 1887), but may con-

tinue until after 2:00 P. M., even on bright days, as I have observed in *B. lenta*. Ernst (1876:35) tells of water guttated by *Calliandra Saman* falling like a fine rain all day.

Root pressure rises rapidly with the temperature of the ground. The bubbles of air in the tracheae enlarge when warm, and, as Sachs points out (1860; Hofmeister, 1862), this will force water upward and may well work with real root pressure in the spring bleeding of grape, maple, etc. I would hesitate to ascribe so much importance to it, however, as does Strasburger (1891:833 *seq.*). If bleeding were very largely due to it the daily periodicity would be reversed, as sometimes occurs, especially near the close of the bleeding season (Hartig, 1863:277; Clark, *l. c.*).

According to Wieler (1893:63) guttation is dependent on the presence of free oxygen. Wieler construes this as an argument that root pressure is caused by differences in concentration maintained within the cell. But Purjewitsch's (1897)² discovery of the great influence of oxygen on diffusion through the protoplasm converts Wieler's point into a better one for the otherwise more plausible theory that root pressure depends on permeability to the solute.

The minor rôle played by root pressure in the ascent of sap is obvious from the limited work possible by any pressure to be observed, and from the fact that it is altogether absent at the times during the season when transpiration is most active. On the latter point enough has been said. As to the pressures, those which I have cited are the highest ever recorded, with the best subjects growing in our climate. With ordinary subjects which show any root pressure at all it is usually only a few centimeters, or only millimeters, of mercury. It is true that the pressure as measured by manometers is an excess over the counter pressure of the atmosphere. Root pressure unable to overcome this can be demonstrated in many plants (Scheit, 1886:701; Wieler, 1893:97 *seq.*) if the atmospheric pressure is

²From instances in which the food normally diffuses from the cell without apparent change, I am unable to agree with Purjewitsch in ascribing the effect of the presence or absence of oxygen to its action on enzymes.

removed; but in living cells, when the gas higher up in the stem is not more dilute than that outside, it must exert a similar resistance of at least an atmosphere to the rising sap. In the spring when root pressure is most active, manometers inserted at different heights show pressures corresponding to columns of water of the same differences in height (Clark; Hofmeister, *Flora*, 1858:4.) So water in the tree, when it practically fills the lumina, will at most be shoved up as far as the same pressure would drive it in a glass tube. As we will see later, this is not necessarily the case when the wood contains a great deal of rarefied air.

III. Let us now turn to the force of attraction. It is a matter of common understanding that the leaves have available practically unlimited energy for the elevation of water if only it can be so applied. Of the radiant energy absorbed by the chlorophyll but a small fraction is used in photosynthesis; and evaporation, by cooling the leaf, enables it to absorb more heat from the air. This energy is nearly all used for evaporation. Whether we say with Mayer (1895:366) that the cause of evaporation is "*die lebendige Kraft der Wassermoleküle durch welche diese geneigt sind Dampfform anzunehmen*," or with Nägeli (1860:38) that the energy is drawn from the tissue itself, it ultimately comes as heat and light from without. Whatever force has been used in drawing water up to the leaves must be overcome when it has evaporated; which slightly decreases the amount evaporated. At the same time, the same force becomes available for the elevation of more water. The energy thus indirectly used in lifting is relatively inconsiderable. In a former note (1900), figuring the latent heat of evaporation, which varies with the temperature, at 536 calories, the mechanical equivalent of a calorie being 424, I pointed out that the energy used in vaporizing water would lift it about 142 miles. At ordinary temperatures the latent heat of vaporization is enough greater to raise this to perhaps 156 miles. Of course, no large part of this could be used in lifting (Rodewald, 1892). Nägeli (1860:39) says that the evaporation uses in general 131

times as much energy as assimilation, which in turn uses eighty times as much as it takes to lift the water; obviously this depends upon how far this is lifted.

It must be almost exclusively true in nature, as Askenasy (1895 : 333) has it in his very clear and concise scheme of the energy changes in the rise of water, that the chief force in the leaf which removes the sap from the tracheae and in spite of which it evaporates, is osmosis. To be complete, it may be said that imbibition intervenes between osmosis and evaporation to get the sap through the wall of the mesophyll cells from which most of it evaporates. On the other side, it also intervenes in the walls between the living contents of the mesophyll and the tracheae from which they draw water. Very likely a little water passes out in the walls from the vessels to the point of evaporation independently of osmosis; at any rate this is not prevented by suberization of the anticlinal walls, as in the endodermis of roots. When water evaporates from a mesophyll cell, the concentration of its sap increases and the tension of its wall is eliminated. In both of these ways, but at first in chief part in the second way, the cell is enabled to draw more water from whence it can, from the tracheae. Mechanically this elimination of the tension of the wall suggests the elasticity of the wall by which Böhm (1864) at first sought to explain suction by leaves; but the actual tension always remains a stretching. In some of his latest work (1890, etc.) the same author denied the play of osmosis on the ground that transpiration is not stopped by death. Evaporation does occur after death, evaporation of the water in the leaves, and of as much more water as can be drawn up before enough air diffuses into the walls and lumina of the tracheae to close them to water; in leaves of firm texture, especially in evergreens, this does not soon occur. But this is not ground for doubting that in living leaves the water passes through the cells, necessarily, by osmosis.

All water passes from the tracheae by imbibition, and so far as the mechanism of movement in the tracheae is concerned, it matters not whether or not osmosis is active in the leaves (Ask-

enasy, 1895; Dixon, 1896; Darwin, in Darwin, etc., 1896: 336-7; Joly, *ibid.* 649). Regarded purely as a transpiring machine, the live leaf is superior to the dead one chiefly because it does not incapacitate itself by drying. Dixon's suggestion (1896, I) is a good one, that dead leaves transpire less than fresh live ones because the collapse of their cells closes the intercellular space. But his other idea, that the fact that flaccid live leaves evaporate only half as much water as dead ones is due to their loss of "turgescence," seems to me to rest on a confusion of the osmotic pressure of the solutes in the cell sap—which I have tried (*Annals of Botany*, June 1902) to distinguish as "turgor"—and the state of "turgescence" caused by the "turgor" when enough water is available. It is by virtue of its "turgor" that the mesophyll absorbs water from the tracheae; and the "turgor" is greater, because when the cell shrinks its sap becomes concentrated, in flaccid than in fresh leaves.

The osmotic pressure in the leaf cells is much more than is used in lifting water. From very numerous tests by plasmolysis I can say that it is in general about equivalent to that of 3.5 per. cent KNO_3 . In some plants it is much higher; for instance, in grasses and in halophytes. In typical spongy parenchyma the turgor cannot be accurately measured. In the bundle sheath it seems usually to be slightly less than in the palisade tissue, but this may be because the tests of the latter is less accurate. It also seems to be on the whole a little higher in trees than in herbs, but this also may be because the cells are usually smaller in trees, making the turgor appear too high. Dixon (1896, II) has undertaken to measure the turgor of leaves by ascertaining the gas pressure sufficient to collapse the cells and force water from them into the tracheae. The method is not a reliable one until we know something about the passage of the gases into solution and their diffusion into the cells. We have no information as to the turgor in the leaves of very high trees, 60 to 150^m in height, but to lift the transpiration stream it need not be higher than that of herbs.

The mesophyll cells supply themselves with water from the

fibrovascular bundles, whose finest ramifications are fine tracheides.

IV. So far, the mechanism of the movement of water is a very simple problem. The difficulty is in the next step, in explaining how suction in the tracheides and vessels of the leaves can be propagated so as to cause an upward movement along the stem, and even from the roots of lofty trees. Summarizing a part of our empirical knowledge may facilitate a subsequent analysis of the theories. The path of the transpiration stream is, speaking for trees, in the younger wood. The number of years' growth of gymnosperms and dicotyledons which share in conducting it is very variable. Beside this radial limit, the stream supplying any particular part of the crown — as a single branch — is also limited tangentially. A well-known experiment by Th. Hartig (1853: 313) illustrates this. He bored five holes in a tree, meeting in the axis, and filled the cavities with "holzsaurem Eisen;" the tree was afterward cut forty feet higher up, and the figure of a star, one ray corresponding to each hole found stained. Experiments on the lateral movement of water by overlapping cuts from opposite sides date back to Hale's. As on various other points, the most valuable collection of data is Strasburger's (1891: 595 *seq.*; 1893: 34, 37). Other more notable work on transverse movement is by Darwin and Phillips, Vesque (1883, 1891: 576), Wiesner (1875). A limit to the ease of lateral movement is necessary in order that any store of water can be retained, while other water moves past it from the ground. It is also necessary for the maintenance of any proportion of air and water in the individual channels.

With the exception of a time in spring when the lumen of some trees becomes full of water forced there by root pressure, the tracheae always contain a considerable amount of air. Scheit maintains that the spaces in the lumen not occupied by liquid water are filled with its vapor, and Sachs in his latest work (1892) inclines toward the same view. But before Scheit's time there was abundant proof of the presence of air, including analyses by Böhm (1878), Faivre and Dupré, and others; and more

recently it has been redemonstrated by Schwendener (1886 : 563), Tschapolwitsch, and Strasburger (1891 : 677). The air content of the heart is rather fixed, but that of the sap wood decidedly variable. With only the same class of exceptions as to the presence of air at all, the air in the tracheae is under a lower tension than that of the atmosphere outside. This lower tension is one of the reasons for the presence of air in the gaseous form. The water absorbed by roots is saturated with air under the atmospheric pressure and at ground temperature. In the trunk the water is usually warmed and a part of the pressure is removed, both tending to cause the air to come out of solution. It has not been so easy to tell why there is not more air in the wood. But Noll's recent discovery that there is an active osmotic movement of gas between the wood and the air outside throws an altogether new light on this question. At least for vessels in or near the leaves, Noll shows that this osmosis will be very largely outward. Before this discovery, the only known immediate cause of the diminished tension of the tracheal air, aside from the relatively inconsiderable influence of occasional cooling, was the removal of water from the lumina to replace that evaporated from the leaves.

The less air the tracheae contain, the greater will be the change in its tension with a given variation in the amount of water present. Evidently the proportion of water present gives an approximate, though not an exact measure of the tension of the air. This proportion of water is in all cases least in summer, the maximum being in winter in gymnosperms, and in spring in dicotyledons (Th. Hartig, 1868 ; Geleznow, 1876. R. Hartig, Bot. Zeit. 1883, disputes this). Th. Hartig (*l. c.*, 20) tested the water content of twenty-six kinds of trees, four feet from the ground, before sunrise, and at 2 : 00 P. M., and found the loss of water varying from 2 to 38 per cent. G. Kraus' most accurate work on this subject comes to the same conclusions, epitomized by Kraus himself in Sachs' *Pflanzenphysiologie*, second edition p. 601, as follows : "Die Pflanzentheile (Stämme, Blätter, Früchte, Knollen, Knospen) . . . sind am Tage kleiner, bei Nacht grösser."

“Diese An- und Abschwellung resultirt aus dem periodisch schwankenden Wassergehalt der Theile; dieser ist regelmässig am Tage geringer, in der Nacht höher.” “Der ungleiche Wassergehalt der Organe bei Tag und Nacht ist seinerseits das Resultat aus der ungleichen Thätigkeit der Wasser zu- und abführenden Kräfte.” We will return later to the tensions associated with the water content. The rarefaction of the gas in the tracheae is often spoken of as causing a negative tension. The physical condition of a gas makes it impossible that it should exert or even transmit a real negative tension. A gas must always press against whatever confines it; when the gas is rarefied the pressure diminishes, but it can never become a suction.

While lateral movement of water in the wood is difficult, its passage lengthwise of the wood is exceedingly easy. This is easily and conclusively shown by what is known as the “Th. Hartig experiment.” As an instructive experiment, we owe this to Sachs; but no one experiment can be identified as “Sachs’ experiment,” so the misnomer can profitably be retained. As a matter of historical interest it may be remarked that the experiment did not originate with Hartig. Boucherie (1841) had made a technical application of it in substantially the same improved form afterward employed by Sachs. And Biot (*cf.* Biot, 1841) preceded Boucherie, but I have not had access to his earlier papers. Hartig showed that when water was forced out of a stick by warming it, gravity could determine the place of its appearance. Sachs’ familiar experiment is to soak a stick in water, dry the ends, place a drop on the upper end, and observe that it is absorbed, while a corresponding drop emerges below. Various woods make good subjects for this experiment, those containing vessels allowing the freest movement. As interpreted by Godlewski (1882: 585-7), it shows that the weight of the water held in the wood is sufficient to overcome the resistance to its movement. Schwendener (1886: 579; also Strasburger, 1891: 773) showed that much less than this pressure is required. Strasburger also showed that an excess pressure of only 20 per cent. is required to cause a movement in sticks of

Acacia as rapid as that of the transpiration stream. Too much air in wood hinders or prevents the movement of water, as proven by Boucherie and many of his successors. It is for this reason that shoots cut in air wilt though the cut end be afterwards placed in water; the lesser tension in the tracheae causing those exposed to fill with air at the outside tension. On the other hand, when the vessels are well supplied with water, the removal of part of it facilitates its movement in response to the "attraction" above—according to Dutrochet. It is my belief that in lofty trees it would be impossible for water to be drawn from the root while the tracheae are even approximately full of it; though of course all that is certain or can be demonstrated empirically is that there is a great deal of space occupied by gas when transpiration is rapid.

In a capillary tube filled with a succession of bubbles of air separated by water (Jamin's chain), the resistance to the movement of the entire column of air and water is very considerable (Jamin, Schwendener, and Steinbrinck). While measurements made in glass tubes are not valid for the tracheae (Strasburger, 1891:815), the movement of the bubbles in the latter is interfered with by the sculpturing of the walls and the remains of the partitions (Kamerling, 1898, I: 978). The result is that a pressure insufficient to move the bubbles will cause a flow of water between the bubbles and the wall.

Vesque (1882; Ann. Sc. Nat. 1883) and Capus observed under the microscope that bubbles did not prevent a current above and below them in the same vessel. Vesque (*cf.* 1891: 384; the original publication was in the *Annales Agronomiques* **11**: 1885) afterward determined that this current passed between the bubble and the wall; which was confirmed by Strasburger (1891:703). Pappenheim (1892:161) was unable to demonstrate such a movement; nor could Schwendener, who denied its possibility (1886; 1892:920). I have not found Vesque's experiments exceedingly difficult, either in glass tubes or in tracheae, and will describe some of them briefly later in this paper. The same phenomenon can be conveniently observed in

the rhizoids of the Marchantiaceae. As we are told by Kamerling (1897 : 12), after a bubble is formed in one of the "pegged" rhizoids, it may increase in length downward as well as upward, the water from the lower end flowing past the bubble. Another of Strasburger's experiments (1891 : 819) furnishes as positive proof as that by direct observation; the same experiments which proved that the Jamin's chain was held less firmly in tracheae than in glass showed that a pressure insufficient to move the bubbles would force water through the same tracheae.

V. Some of the theories as to the rise of water, and retaining only an historical interest, may be mentioned very briefly. Knight (1801 : 344) ascribed the ascent of sap to contraction by the medullary rays, "the silver grain," which somewhere touch all the vessels. "Their restless temper, after the tree has ceased to live, inclines me to believe that they are not made to be idle whilst it continues to live." If a tangential surface of wood is exposed during the day, the silver grain appear as minute clefts into which pins may be stuck and be found pinched fast at night. This contraction, he thought, might elevate the water.

Bischoff (1836, Vol. II, pt. 1: 238, 271) believed the sap to be driven up, not in the vessels but in the cells, by the contractility of the walls, acting under the influence of the living contents. Böhm at one time (1878) held a similar view, omitting, however, as he always did, any dependence on the activity of the protoplasm. He called the movement (p. 230) "*une fonction de l'élasticité des parois cellulaires et de la pression atmosphérique.*" But already in the same paper (p. 236) he recognized that in cells with rigid walls their elasticity is replaced by that of the air in the lumen.

Th. Hartig (1853), observing facetiously that his was the age of steam, thought the cavities of the pits might act as millions of little engines so numerous that when warmed even a very little they could drive the water up.

The agitation of trees by the wind was plausibly used by Spencer to move water in the vessels from the roots, where it was most abundant, to the twigs and leaves where evaporation

created a constant demand; the arrangement being "a sort of rude force-pump worked by the wind."

Scheit suggested that slight differences in temperature might raise the water "auf dem Wege der Destillation" (1885:477). But, as Scheit himself pointed out, this would not raise any mineral food.

VI. While the imbibition theory has had no champion since the death of Sachs, it reigned too long to be passed over in a sentence now. Granting Sachs' claim that the imbibition theory was his personal intellectual product and property, it would seem but fair to confine ourselves in discussing it to the final stage of its evolution. But it was in one of its earlier forms, afterward outgrown by its great exponent, that the theory was dominant. Sachs lists the publications in which this theory was developed in his hands in his *Vorlesungen über Pflanzenphysiologie* (2d edition, 225). Its period of greatest vogue was about the close of the seventies, after the publication of the paper "Ueber die Porosität des Holzes." The imbibition theory said that the water was carried altogether in the walls of the wood elements, where it was absorbed and held by imbibition. The substance of the wood walls was believed to be very remarkable, in "Dass sie (the walls) verhältnissmässig nur wenig Wasser in sich aufnehmen, dass dieses wenige Imbibitionswasser jedoch in ihnen auffallend beweglich ist." The removal of any water from the wood at the top of the tree caused a flow toward the point of loss, the demand for water being thus propagated in the walls to the roots, where it could be satisfied. It had been demonstrated that the forces at play in imbibition far more than sufficed for the elevation of the water; that the water moved easily in wood was certain. That it moved in the walls seemed to have been demonstrated by direct observation of air filling the lumina; by the experiment of Unger (1868), who injected the lumina with wax without preventing the movement of water; and later by Sachs' experiments with sharply bent tendrils, etc.

Sachs elaborated no new theory of imbibition to account for

the movement of water, Naegeli's micellar hypothesis being generally accepted, and accounting satisfactorily for the great force with which the water had to be, and is, held. As I understand the micellar hypothesis, it regards the water as held between the micellae by its surface tension; at any rate, it would say that imbibition and surface tension have a common mechanical explanation. This is not altered in the least by the fact that the presence of the spaces is dependent on that of the water. Since the spaces are indefinitely small, the tension is indefinitely great. In the evaporating surface these spaces become still smaller as they lose water, unless it is immediately replaced from behind, and the menisci formed in them are of such ultra-microscopical minuteness that it is easy to suppose they can draw water higher than any tree reaches. Assuming always that the walls were the path of the water, the imbibition theory was thus complete, and not in open discord with contemporary physical science. As this was not true of any other theory it was but natural that this one was generally accepted, and by a sort of reflex action this strengthened the faith in its premise as to the path.

The identity of imbibition and capillarity was postulated by DeLuc (1791:12), but on evidence—the imbibition of alcohol and ether—which has not been found generally sound. Hofmeister (1862:100) and Unger (1868), who were forerunners in the modern development of the theory, treated them as the same, as did Pfeffer in his unqualified acceptance of this theory in the first edition of his *Physiology*. Naegeli and Schwendener (*Mikroskop*. second ed. 380) say it is indifferent what the force is called, though formulae based on measurements of tubes of appreciable size need not apply in these invisible interstices. In 1865 (*Handbuch*, 213) Sachs entertained no doubt that capillarity and imbibition were related. In 1879 (*Por. d. H.*), however, he regarded the phenomena as distinct, and afterward became most insistent on the difference. This robbed the imbibition theory of its foundation in established physics, and it is very doubtful if it ever could have obtained general credence

in this form. The imbibitionists never offered any physical explanation of the supposed absence of high friction in the fine pores of the wood; this was dismissed as a "natural property" of the wood substance.

The imbibition theory fell with the disproof of its first premise, that the water moved in the walls. Unger's injection experiment was repeated with the opposite result. Elfving (1882:714) plugged the lumina of pieces of wood with cocoa butter and could force no water through them. Scheit (1884) injected sticks with gelatin with the same result. Vesque (1884:188) injected the tracheae of a living branch with cocoa butter and the branch wilted. Errera (1886, I, 31, II) repeated this experiment using gelatin; as did also Strasburger (1891:541). Dixon and Joly (1895) employed gelatin, paraffin, ice, and water vapor to obstruct the lumina, causing wilting in each case. Smith found the movement of water in cucumber stopped or very nearly so by injection with gelatin; the plugging of the spiral vessels by *Bacillus tracheiphilus* caused a gradual wilting, while *Fusarium niveum*, which fills the pitted vessels as well, causes a sudden collapse of watermelon foliage. Vesque (1884), Kohl (1885), and Darwin and Phillips (1885:366) made plants wilt, or checked the absorption as measured by the potometer, by squeezing them until the lumina were presumably closed. The old observation (DeVries) that if a transpiring branch is cut in the air it wilts was recognized as showing that plugging the lumina with air closed the path of the water (Scheit, 1886:172). Against the experiments with bent branches it was pointed out by Russow (1883:99) and Scheit (1884) that bending does not entirely close the lumina. And Dufour's inability to force water through the bends under pressure was ascribed by the opponents of his theory to the entrance of air where his wood was exposed in cutting.

The movement of water in the lumina was directly observed by a number of investigators, notably Vesque. The well-known presence in the lumina of colors and other substances used in detecting the path of the transpiration stream had been ascribed

to the abnormal direct atmospheric pressure against cut surfaces ; but without reason, as Van Tieghem (1870:278 *seq.*) found decoctions absorbed by sound seedlings of Leguminosae confined to the lumina of the vessels. Once the imbibition theory was undermined, older objections to it, some of which Böhm had been constantly raising, were granted recognition. It was incontestable that lumina of at least a part of the conducting elements contained water ; the imbibition theory could offer no explanation at all of its presence (Böhm, 1878:225 ; Sachs, 1887:247). The absence of a parallel between transpiration and absorption (McNab, 1874:356 ; Vesque, 1878) was therefore unintelligible to imbibitionists. The excessive difference in the facility of transverse and longitudinal movement of water was not intelligible on the basis of the distribution of the water of imbibition, the difference in other physical properties of the wood walls being relatively small. The drying out of dead branches of living trees would seem impossible according to the imbibition theory. And there are other minor objections to it which need not be touched upon here.

Our permanent debt to the founders and supporters of the imbibition theory is for placing great emphasis on the easy passage of water through the wood,³ and for suggesting a physical means for this passage. The water cannot escape passing through occasional walls as it rises. And the work of Errera and of Dixon and Joly, already cited, testifies that some water, though far from enough to satisfy the demands of transpiration, can travel in the walls for a considerable distance.

VII. An active rôle in the elevation of the water has been ascribed by many writers to capillarity in the lumina of the elements of the wood.⁴ At the same time it has been recognized

³Even this is disputed by Janse.

⁴Recognizing of course that capillarity is not an ultimate source of energy for the rise, but that this is furnished when the water is evaporated. It would indeed be a careless attempt at an explanation which should seek in capillarity the energy to keep a stream moving upward ; still, I cannot agree with Kamerling that this would be a "logical error," since the law of the conservation of energy does not itself rest on logic.

that in tubes of such size as these lumina the lifting power of capillarity is not exceedingly great. In a glass tube 10μ in diameter this should be about 3^m . Strasburger (1891:87 *seq.*) found it less in tracheae than in glass, sometimes less than half as much. While the lifting power is determined by the form of the meniscus, it is possible enough that this should be influenced by the nature of the wall. In the absence of direct contrary evidence on the same subject, which is wanting in Schwendener's criticism (1892:912), Strasburger's statement must stand.

The efficacy of capillarity is limited again by the dilution of the air in the tracheae. Naegeli's classical work on capillarity (1866, I, II) showed experimentally that with diminishing atmospheric pressure the lifting power of a meniscus in a glass tube decreases; slowly at first, but rapidly when the pressure approaches zero. The theoretical ground for this is evident from the intimate connection between surface tension and vapor tension. Naegeli found the details to be remarkably dependent upon the temperature. Since the air in the tracheae is always rarefied when transpiration is at all active, and with excessive transpiration the loss of pressure is great enough sometimes to lead to the formation of bubbles of water vapor, the service which capillarity can perform in the elevation of water is most insignificant when the demand for water is most urgent. A repeated, but so far as I can see entirely unwarrantable assumption (Böhm, *Ann. Sci. Nat.* 1878:232; Elfving, 1885:536; R. Hartig, *Bot. Zeit.* 1883; Sanio) has been that each wall across the path of the transpiration stream furnished a fresh starting point for capillarity to work from. There is no reason why a wall should offer any greater resistance to movement of water downward in response to gravity than upward in response to capillarity.

The Jamin's chain has never been shown to have any advantage over a single meniscus in causing a movement of water. For every added meniscus with an upward pull there is one of the same shape whose concavity is downward. The resistance

offered by a long series of bubbles to longitudinal pressure has given the Jamin's chain a place in some theories (Westermaier, 1883; also Hartig, 1882; Vesque, 1884), as an arrangement to hold the water up, forces of a different nature being invoked to elevate it. Statements as to this resistance of the "chain" in glass tubes are very discrepant (Janse; Naegeli, Plateau — as cited by Strasburger, 1891: 815 — Zimmerman, 1883); according to the experimental results of Schwendener (1886: 569) and Strasburger (1891: 819) the resistance to the movement of the chain as a whole is not usually very great in tracheae.

If the pressure against the upper end of such a column of air and of water were diminished or removed, the result would obviously be an elongation of the bubbles, lifting the water supported by them. This would operate most at the top, and would cease at a point down the column where the resistance to the bubble's expansion was equal to its excess of tension. In this way Schwendener (1893) thinks it likely that the diminished tension in the vessels might be able to lift some water as much as 15^m instead of the 10^m to which a pressure of one atmosphere could lift an unbroken column. Under certain imaginary conditions, which as Schwendener showed do not really occur in plants, a much greater height would be possible; Schwendener (1892: 934) suggests such a case in which the bubbles should be 10^{mm} long, in which Steinbrinck (1894: 127) showed that the top of the column might be lifted 142^m. As to the actual length of the bubbles, Schwendener puts the average in *Fagus* at 0.33^{mm}, that of the supported water being 0.14^{mm}. Both Schwendener and Steinbrinck seem to assume in their calculations that a meniscus will retain its full effectiveness in a vacuum, which, as has just been pointed out, is not at all the case. Moreover, such a mechanism, in lifting water, would accumulate air at the top, and so destroy itself, and therefore (Askenasy, 1895), even if it could lift water once, it could not raise a constant stream.

During the last decade surface tension has been playing a very prominent part in still another form in explanations of the ascent of sap. The cohesive power of pure water was demon-

strated by Naegeli and interpreted with an insight in advance of his time. He says (1866:498) "Viele Versuche zeigten, dass in frisch gezogenen Capillarröhren die Spannung negativ werden kann, ohne dass in dem ausgekochten Wasser Dampfbildung eintritt;" thus in one experiment the cohesion of the water sustained a mercury column 44^{mm} in excess of that in the barometer. Two other sentences outline Naegeli's interpretation: "Dieses Entzweireissen einer Wassersäule ist im Grunde nichts anderes als Dampfbildung in derselben⁵;" and concerning the amount of resistance to such pulling apart, "Es wäre selbst möglich, das es dafür keine Grenze gäbe." Böhm cites Helmholtz on this same point, the passage referred to (1874:492) being on cohesion by very dilute sulphuric acid. Böhm himself in 1890 (*Bot. Centralb.* 268) found that *Salix* with boiled roots would absorb water and draw up mercury "Stets bis zur Barometerhöhe," when the total pressure of mercury in the water must have been above one atmosphere. Strasburger (1891:792) got the same result with branches of *Taxus* and *Tsuga*. Böhm then (1893:209) reported the lifting of mercury columns 22^{mm} above that of the barometer by *Salix*, and 161^{mm} above it by *Thuja*. In this paper Böhm seems to refer repeatedly to cohesion when he speaks of capillarity.

A little later than this, Askenasy (1895) published an exceedingly clear theory on the ascent of sap, in which the chief rôle in making the pull set up by evaporation in the leaves operative at indefinite distances down the trunk was ascribed to the cohesion of the water. The priority of the publication of most of this theory belongs to Dixon and Joly, who published abstracts of their work in 1894. The general acceptance of it is due more largely to Askenasy, whose name is usually associated with it. So is Strasburger's name, though he has not publicly subscribed to it, and it is not in harmony with all of his work. Like the imbibition theory, this one was complete in that the premises, proven and assumed, were an adequate foundation for the conclusion; the factors, as the theory used

⁵ Physicists are not agreed on this.

them, were equal to their work. Its acceptance was naturally prompt and widespread, giving a new interest to the study of the cohesion of water from the physical side. Askenasy (1896: 441) was able to draw up mercury 82^{cm} and again 89.3^{cm} by a pull resulting from evaporation from a plaster of Paris surface. Dixon and Joly (Trans. Roy. Soc. 1895: 570), by a method better calculated to indicate very great tensions, demonstrated that columns of water could endure a longitudinal pull of more than seven atmospheres before breaking, and that this was possible without absolute freedom from gas, and with bits of *Taxus* wood in the water. By the same method Berthelot had obtained negative tensions, since variously estimated at 50 to 150 atmospheres. There is a résumé of some other work, including some of Lehmann's own, in his *Molecularphysik* (I: 243-5), in which Naegeli is overlooked. Kamerling (1898: 465) showed on theoretical grounds, the same as Naegeli's must have been, that in pure water *at rest* the resistance to pull must be infinite.

The supposed difficulty with other theories which the cohesion theory sought to overcome was their failure to provide for the transmission of really negative tensions, *i. e.*, tensions more than one atmosphere less than the normal. So long as the tension remains positive there is no possibility of the exercise of cohesion; the least positive tension would itself prevent a rupture of a column, whether of water or of water and air. But it is argued that water can be lifted 10^m at most while its tension remains positive; that when it is lifted higher, as in trees everywhere, negative tensions *must* be present near the top. There are two easy ways of determining empirically the opportunity for the play of cohesion in the plant: measuring the tensions actually present, and testing the result of artificially established tensions.

We have already mentioned that the tension of the air is ordinarily less than one atmosphere, and of course that of the contiguous water is the same. Well known to older writers, but too little considered, this fact came strongly to the fore with v.

Höhnel's work (1879). He found (p. 113) that a suction of 40–50^{cm} Hg was not rare as late in the year as the end of October. Böhm (1877) found a suction by *Crataegus* of 61^{cm}; by *Syringa* and some *Pomaceae* of 25^{cm}; and by *Platanus* of only 16^{cm}; and (Bot. Zeit. 1881: 824) even in March a suction by *Crataegus* of 40^{cm}. In one experiment (Bot. Zeit. 1881: 819) mercury was jerked into a vessel of *Robinia* 117^{cm}, but this was not a rise of that distance.

In 1890 Böhm said that *Salix* with boiled roots would exert a suction sufficient to lift mercury, as already quoted, "Stets bis zur Barometerhöhe." In 1893 he said that it was in "successful" experiments that the mercury could be drawn as high as the barometer by shoots whose lower end had been cooked; but only three experiments in 400 succeeded. In one of these three the indicated suction was 2.2^{cm} over an atmosphere. We have already noted his results with conifers. Strasburger (1891: 787) reports as the greatest observed suction in any herb 28^{cm} Hg (*Amaranthus caudatus*); in live branches of dicotyledonous trees, 54^{cm}; in branches whose lower end was boiled, 67^{cm}; and in conifers similarly treated, 70^{cm}. Vines (1896) reported suctions of 116^{mm} and of 11 inches by *Helianthus annuus*, 320^{mm} by *Prunus Laurocerasus*, 21¼ inches by *Fagus sylvatica*, and 22¼ inches by *Taxus*. These pressures are to be subtracted not from zero, but from one atmosphere (Vines, Annals of Botany 10: 644). Data obtained by Th. Hartig, Schwendener (1886), and others, by inserting manometers in the trunks of transpiring trees, agree that tensions of zero are not closely approached. A part of these figures may be lower than they should be, because they only indicate the point at which air came out of the cut end of the stem and prevented the absorption of any more water.

On the other hand, figures obtained after removing air by boiling or sucking it out of the cut end are likely to be too high. There is no doubt that the transpiring cells could draw water from the tracheae in spite of an absolute pull; that tensions of zero or less are not transmitted and used to absorb water 15

because the air in the tracheae expands until finally it closes them to the passage of water. Removing a part of the air makes a lower tension necessary for what is left to plug the tracheae and so permits more than the normally possible suction. I have illustrated this with a small branch of a greenhouse grown *Eucalyptus*, the cortex removed, inverted so that when any bubbles were drawn from the stem they could not stay in contact with it and prevent the absorption of more water. It was in air-tight connection with a tube 1^{mm} in diameter, full of water and standing in mercury. The mercury rose in one hour and fifteen minutes 101^{mm}, where it was stationary. This suction was increased to 191^{mm}, but drew air from the pith and wood, and fell slowly to 106^{mm}. A little air continued to be extracted, but the suction increased, until 52 hours after the experiment began it was 173^{mm}; and after 79 hours 235^{mm}. The rise of mercury had become very slow, and at this point a leak stopped the experiment. The young leaves, up to those more than half grown, were already becoming dry, though the cut end was, and had constantly been, in water. It is because the possible suction is chiefly a function of the air in the tracheae that Vines (1896: 538) finds that a large part of the leaves may be removed from a branch without much effect on the suction. For the same reason—because a part of the tracheae are closed—a suction of less than the greatest the transpiration stream can exert may nearly stop the absorption of water (Vesque, 1884; Strasburger, 1891: 788). It seems clear to me that the evidence we have warrants the conclusion that the tensions in the tracheae of living plants—at least of dicotyledons—in nature are never even approximately as low as zero.⁶

What happens if the tension is artificially lowered? Böhm (1864: 546) put more than a hundred *Salix* cuttings in a vessel where the pressure against the absorbing ends was reduced to 8 to 10^{mm} Hg. The result was “Dass die Blätter nach zwei oder höchstens drei Tagen vertrocknet waren. Das Absterben

⁶This was treated as an established fact by Naegeli and Schwendener (1877: 380).

erfolgte in der Regel bei kleinen Reichbeblätterten Pflanzen schneller als bei grösseren wenig beblätterten," etc. Böhms conclusion (562), "Dass die zum Saftsteigen erforderliche Kraft von dem Luftdrucke geliefert werde," is equivalent to saying that an actually negative tension cannot be exerted to absorb the water. Vesque (1884), working with sound water cultures of oleander, found that the absorption became impossible when the tension was one atmosphere *minus* 63^{cm} Hg. Strasburger (1891:793), Scheit (1886, II), and Janse (1887:3-10) all agree that dicotyledons wilt if water is available under too low a pressure, and that the removal of nearly the whole atmospheric pressure always makes it too low. Saussure (p. 30 of Ostwald's *Klassiker* no. 16, p. 214 of original) describes a somewhat different experiment explicable in the same way; vessels containing plants with their roots in water were placed *in vacuo* and lived for weeks, and even grew, if protected from direct illumination. Under the conditions the plant was in an atmosphere saturated with water and did not transpire. Water may have diffused rapidly enough to supply the demands of what growth occurred in a "vacuum." In direct light the plants dried up, because the leaves became warmer than the air, and water evaporated from them and could not be replaced.

We have found not only that negative tensions do not occur in dicotyledons in nature, but that an artificial elimination of the positive tensions to which they are accustomed robs them of the power to absorb and elevate the transpiration stream. There have been some premises and *a priori* arguments for the cohesion theory which, for the sake of thoroughness, we will still consider. Berthelot says (p. 332-3) "À ce moment (when negative tension has been caused by cooling) le moindre choc ou broissement, la moindre vibration fait reparaître à l'instant, avec une sorte d'ébullition, un léger bruit et une secousse plus ou moins notable, le gaz dissous dans l'eau." Lehmann (p. 244), speaking of water under a tension of one atmosphere *minus* 1,200 ^{mm} Hg, says "Erst bei erschütterungen folgt in solchen Fällen das Sinken zum normalen Standpunkt." Donny seems to be

alone (according to Lehmann) in reporting that a jar did not instantly release any negative tension, and his tension was only that of one meter of water. Trees are almost never absolutely at rest; their very agitation by the wind has served once (Spencer) to explain the rise of water. Kamerling, in the same mathematical argument showing that the cohesion of pure water at rest is not limited, proves that the kinetic energy of moving water may easily pull it apart. The transpiration stream not only moves, but moves irregularly, which no negative tension could survive. Because trees are not at rest and the transpiration stream is in unsteady motion, we must regard any negative tension in it as *a priori* impossible.

While Dixon and Joly (1895:571) regard a continuous column of water as an essential assumption in their theory, and base it on Strasburger's statement that there is very little air in the youngest wood, Askenasy, adhering more closely to Strasburger, recognizes that the presence of some air is not an effective bar to the movement of water in the same tracheae, and seems to expect cohesion to operate around and past bubbles. I cannot see the possibility. We believe cohesion to depend on the fact that the first break in a column of water must be an infinitely small bubble, whose surface is a meniscus of infinitesimal radius and a correspondingly great surface tension. In the wood bubbles are present of a very appreciable size. When transpiration is most active, and cohesion is supposed to be most necessary, these bubbles stretch and become practically cylinders. Midway up its side the surface of such a bubble is very much nearer that of a cylinder than of a sphere. The surface tension of such a meniscus hardly deserves the name of capillarity; cohesion is out of the question. The low tension of the bubble still further depresses the surface tension.⁷

Capillarity and cohesion are usually names of manifestations of surface tension under different conditions. Applied to its

⁷In a glass tube open at one end, the shape of the meniscus itself is a function of the tension of the gas; in the case we are considering this is not quite true, because the shape of the tracheae helps to determine that of the bubble.

manifestation in the single fixed set of conditions we have in the tracheae, they are not distinguishable. Ten years ago Böhm alone imagined (publicly) that capillarity could play the leading rôle in the ascent of sap. It had been tried and found wanting. Then it was named cohesion and sprang at once into popular favor.

I have been assuming that the transpiration stream does not rise in tracheae entirely free of bubbles. The evidence for this is unlimited. It was formerly taken as an established fact, and the imbibition theory rested very largely upon it. Since this theory collapsed, Schwendener has shown again by most careful work that when transpiration is active continuous water "threads" are wanting. The experiments of Strasburger (1891:681-6), on which Dixon and Joly rest their case, were obtained in this way: branches were cut, under water if possible, and left standing in shade or darkness for some hours, until they had all the water they would hold; then they were examined and the youngest wood, which is most active in conducting water, was found to "contain very little air," or "the air could be detected with difficulty." It is easy to substantiate this observation. The subject of experiment has absorbed all the water it can, with the help of the whole pressure of the atmosphere, so there is no opportunity for the demonstration of cohesion, however abundant and continuous the water. The experiment gives no clue to the water content and its distribution when transpiration is active and water less accessible, and cohesion might be of service. Hartig (1888) and Wieler (1888), among others, have shown conclusively that it is just in this youngest wood that the water content is exceedingly variable, dependent on the supply and demand. Von Höhnelt (1879:126) found the lowest tension in the youngest ring. And an experiment of Böhm's, already cited, shows that in the case of Robinia, one of Strasburger's few dicotyledonous subjects, active transpiration leaves the vessel far from full of water. The following experiment hits the question squarely; it also covers the other question of movement past bubbles, on which a superfluous amount of evidence is not yet in print.

A young branch of *Eucalyptus globulus*, with ten pairs of expanded leaves, all horizontal, stood in water four hours. The xylem was then full of water, excepting the large pitted vessels which contained bubbles occupying about half of their volume. Both sides of the stem for 2^{cm} were cut away almost half through, leaving only a very thin strip, which was protected against desiccation with vaseline. The structure was so fine that in the outer part of the xylem only the pitted vessels were clear cut and individually distinct. The lower end of the branch was tied into a glass tube containing a little water over a meter of Hg, the other end of which tube was swung down so as to subject the cut end to a pressure of 9^{cm} Hg instead of 74^{cm} (the atmosphere). Within five minutes the water began to disappear from the pitted vessels, which were soon visibly empty. The spiral vessels (primary) were but little later losing their water; while it was more than half an hour before the lumina of the wood fibers became generally empty. During the first part of this time the cut end was in contact with water, the rubber tube connecting the plant with the glass tube being bent 180°, so that air escaping from the branch would not collect against it. The branch used up its stored water, then, not because other water was not at hand, but because it cannot absorb it when the pressure is only 9^{cm} Hg. After about fifteen minutes the subject was kept horizontal under the microscope and very likely water was no longer kept against the cut end. To this point the experiment showed that, as Strasburger found, while the conducting part of the wood fills with water when it may be absorbed under the full atmospheric pressure, its lumina become empty again when this pressure is removed. When the leaves are called upon to exert a great suction, the continuous threads of water whose cohesion might transmit it do not exist.

After the lumina became free of visible water, the suction was removed, and the branch set in water for three minutes. Then eosin was given drop by drop to the cut end. It was eagerly absorbed, showing that the lumina had not filled to any considerable extent with air from outside. Watching for the eosin with the naked eye, it was between four and five minutes before

I detected it in the thin strip; then it had traveled the whole length of it on one side of the pith, nearly the whole on the other. It was absolutely confined to the spiral (primary) vessels, next the pith, and was about equally distributed in three to five layers of these. Twenty minutes later, isolated vessels outside of these (not the pitted ones) were injected. It was exceedingly evident in these isolated vessels, as I had been able to make out quite unsatisfactorily in the inner spiral ones where the whole group was red, that columns of colored water were separated by bubbles. With a high magnification I was able in a few places, where the thickness of the wood did not interfere too much, to see a very distinct red film lining the wall and connecting the indices of red liquid. It must be remembered that these vessels were the first in their immediate neighborhood to carry the eosin. It seems to me that the conclusion is warranted that the bubbles are not an appreciable obstacle to the passage of the water. Strasburger describes exactly the same case.

To summarize the discussion of the cohesion theory: It is applicable only in explaining the transmission of negative tensions; but negative tensions do not occur, nor do the positive tensions present approach zero; the movement of water is prevented by artificially removing the normal positive tensions; if negative tensions could arise they would be immediately released as a result of the movement of the water and the agitation of the trees; more than an insignificant negative tension is impossible in the presence of free gas or a vacuum, as the only bar to the enlargement of the bubble is its surface tension, and this decreases with the pressure; when the tension is low and transpiration is active, there are bubbles in all water conducting elements.

[*To be concluded*].